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# Cladistic analysis of *Simulium* (*Trichodagmia*) and *Simulium* (*Thyrsopelma*) (Diptera: Simuliidae)

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A cladistic analysis of *Simulium* (*Trichodagmia*) *sensu* Crosskey and Howard, using 34 morphological characters of larvae (6 characters), pupa (5) and adults (23), yields nine most parsimonious trees under equal weights (length 101 steps CI 0.49 RI 0.73). Successive weighting based on the maximal rescaled consistency index preferred one of the nine (31.37 steps CI 0.62 RI 0.87 total $fit_{con3} = 235.8$), which was also one of two trees found under implicit weights with concavity values of 3–6. The cladogram justifies the recognition of two subgenera. *Simulium* (*Trichodagmia*) *sensu stricto* (containing *S. muiscorum*, *sumapazense*, *S. wygodzinskyorum*, *S. nigrimanum*, *S. chalcocoma*, *S. huairayacu* and *S. lahillei*) is supported by the branchial tip sclerotization and the presence of cibarial teeth, larval body tegument covered with lanceolate hairs, female with simple claw, and gonapophysis size. *Simulium* (*Thyrsopelma*) (containing *S. scutistriatum*, *S. hirtipupa*, *S. orbitale*, *S. guianense*, *S. perplexum* and *S. itaunense*) is supported by the hypostomial teeth.


ADDITIONAL KEY WORDS: monophyly – neotropical simuliids – equal weights – successive weighting – implicit weights.

## INTRODUCTION

Enderlein (1934) proposed two neotropical blackfly genera, *Thyrsopelma* and *Trichodagmia*. The type species of *Simulium* (*Thyrsopelma*) is *Simulium* (*Thyrsopelma*) *brasiliense* (Enderlein, 1934:284) [= *Simulium orbitale* Lutz 1910:231]. The type species of *Simulium* (*Trichodagmia*) [= *Simulium* (*Grenieriella*) Vargas & Díaz Nájera 1951:141] is *Simulium* (*Trichodagmia*) *latitarsis* (Enderlein, 1934:288) [= *Simulium chalcocoma* Knab, 1914:85]. Both species descriptions were based only on females.

Coscarón (1987, 1991) considered *Thyrsopelma* and *Trichodagmia* as two distinct taxa based on the form of the female genitalia, hairs of the larval tegument, and the arrangement of hypostomial teeth. At that time, he used the name *Grenieriella* instead of *Trichodagmia* because *Simulium lahillei* (Paterson & Shannon, 1927; type of *Grenieriella*) was known from all life stages. He recognized three species groups within each taxon: *scutistriatum*, *hirtipupa* and *orbitale* within *Thyrsopelma*, and *lahillei*, *nigrimanum* and *muiscorum* within *Trichodagmia* (Coscarón, 1987). Crosskey & Howard (1997) recognized just one taxon, synonymized *Thyrsopelma* with *Trichodagmia*, and did not recognize any species groups.

*Trichodagmia sensu* Crosskey & Howard (1997) formerly comprised 15 species [*albopictum* Lane & Porto, 1940; *argentatum* Enderlein, 1936; *chalcocoma*, *guianense* Wise, 1915; *hirtipupa* Lutz, 1910; *huairayacu* Wygodzinsky, 1953; *itaunense* d'Andretta & González, 1964; *lahillei*, *muiscorum* Bueno, Moncada & Muñoz de Hoyos 1979; *nigrimanum* Macquart, 1838; *orbitale*, *perplexum* Shelley, Maia-Herzog, Luna Dias & Couch, 1989; *scutistriatum* Lutz, 1909; *sumapazense* Coscarón & Py-Daniel, 1989 and *wygodzinskyorum* Coscarón & Py-Daniel, 1989]. Coscarón (1991) considered *S. albopictum*, based on three females from Cambara

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**Table 1.** Character list and states

LARVA

0. Larval antennae: smooth [0]. with secondary annulation [1].
1. Hypostomium central and intermedial teeth: well differentiated [0] not well differentiated [1].
2. Mandible apical tooth: not-reduced [0] reduced [1].
3. Anal sclerite hook number: 1–99 [0]; 100–149 [1]; >150 [2].
4. Anal gill diverticula number: 0 [0]; 1–5 [1]; 6–20 [2]; >21 [3].
5. Body tegument: glabrous [0];with simple hairs [1]; with lanceolate hairs [2].

PUPA

6. Branchial filament number: 1–6 [0]; 7–10 [1]; 11–20 [2]; >21 [3].
7. Branchial tip form: rounded [0], sharp [1].
8. Branchial tip sclerotization: slight (clear tips) [0]; medium [1]; strong (dark tips) [2].
9. Tergites VI to IX: with a basal spine comb [0]; without a basal spine comb [1]; spine comb only in the penultimate segment [2].
10. Terminal spines: well developed [0]; reduced or absent [1].

FEMALE

11. Cibarium: unarmed [0], armed [1].
12. Cibarium: with acute teeth [0]; with small tubercules [1].
13. Claw: simple [0], with a small sub-basal tooth [1], with a well-developed sub-basal tooth [2].
14. Wing length: 0–1.79 mm [0]; 1.8–2.5 mm [1]; >2.51 mm [2].
15. Subcostal vein (Sc): glabrous [0]; hairy [1].
16. Radial vein: basal sector (Rb): glabrous [0], hairy [1].
17. Paraproct distal portion: sclerotized [0], membranous [1].
18. Paraproct form: subcircular [0], subquadrangular [1], rectangular or ventrally produced [2], digitiform [3].
19. Paraproct length/width ratio: 0–1.49 [0], >1.5 [1].
20. Paraproct microtriquies: covering the entire paraproct [0], only in the distal border [1].
21. Paraproct spicules: slender [0]; robust [1].
22. Genital fork arms: Not very expanded distally [0], very expanded distally [1].
23. Genital fork arms: with prominent internal projection [0], without internal projection [1].
24. Spermatheca: flat [0], sculptured [1].
25. Gonapophysis shape: subtriangular, apically rounded [0], subovoid [1], acuminate, apically produced [2].
26. Gonapophysis length/width ratio: length = width [0], length>width [1], length<width [2].
27. Basimere length/width ratio: 0–0.65 [0], more than 0.66 [1].
28. Distimere length/width ratio: 0–1.0 [0], 1.01–2.8 [1], >2.81 [2].
29. Distimere apex: straight [0], very bent [1].
30. Ventral plate scotadures: Inverted U shaped [0], H shaped [1].
31. Ventral plate distal border: rome [0] carenate [1], depressed [2].
32. Endoparamere: with teeth [0], reduced or absent teeth [1].
33. Endoparamere teeth: similar in size [0], small and large teeth [1].

(Parana, Brazil), and deposited in the School of Saúde Publica of Sao Paulo University (Brazil), as a species *inquierandae* and possibly a junior synonym of *S. pintoi*. The latter species was later synonymized with *guianense* by Crosskey & Howard (1997). After examining the syntypes of *S. albopictum*, we concluded that the scutum pattern and general colour of *S. albopictum* is sufficiently similar to *S. guianense* to maintain the synonomy of both *albopictum* and *pintoi* with *guianense*. This synonymy could be reconsidered if male, pupal and larval stages of *S. albopictum* are found. Coscarón & Miranda-Esquivel (1998) synonymized *S.* (*Trichodagmia*) *argentatum* with *S.* (*Inaequalium*) *inaequale*. These synonymies reduce the total number of species to 13.

*Thyrsopelma sensu* Coscarón occurs from the southeast of Brazil to Amazonia, the Guyanas and southern Venezuela (*guianense*), and west to Paraguay and eastern Argentina (*orbitale*). Some species of *S. Thyrsopelma*, such as *guianense* shows high anthropophily. Indeed, it is an onchocercosis vector in Amazonia; *orbitale* and *scutistriatum* are known as a nuisance to humans and cattle. *Trichodagmia* occurs throughout western South America, from Colombia to central western Argentina. *S.* (*Trichodagmia*) *nigrimanum* is con-

**Table 2.** Data matrix. Data set used in the analysis. All characters coded as unordered. '?'=Unknown. '–'= Inapplicable

| Taxa\Characters | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *PARAAUSTROSIMULIUM* | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 | 0 | 0 | 0 | 0 | – | 2 | 2 | 1 | 0 | 0 |
| *NEVERMANNIA* | 0 | 0 | 0 | 0 | 1+3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | 1+2 | ? | 1 | 1 | 0 |
| *POMEROYELLUM* | 0 | 0 | 0 | 0 | 0+1+2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | – | 2 | ? | 1 | 1 | 0 |
| *PTERNASPATHA* | 0 | 0 | 0 | 0 | 1+2 | 0+1 | 0+1 | 0 | 0 | 0 | 0 | 0 | – | 2 | 2 | 1 | 0 | 0 |
| *S. oviedoi* | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | – | 1 | 1 | 1 | 0 | 0 |
| *HEMICNETHA* | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | – | 2 | 1 | 1 | 0 | 0 |
| *HEARLEA* | 1 | 0 | 0 | 2 | 2 | 0 | ? | 0 | 0 | 1 | 1 | 0 | – | 1 | 0 | ? | 0 | 0 |
| *ANASOLEN* | 0 | 0 | 0 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 0 | – | 1 | 2 | 1 | 1 | 0 |
| *XENOSIMULIUM* | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | – | 1 | 0 | 1 | 1 | 0 |
| *FREEMANIELLUM* | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | – | 2 | 2 | 1 | 1 | 0 |
| *S. muiscorum* | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 1 |
| *S. sumapazense* | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 | 1 |
| *S. wygodzinskyorum* | ? | ? | 0 | 2 | 2 | 0 | 2 | 1 | 0 | ? | ? | ? | ? | 2 | 2 | ? | 1 | 0 |
| *S. nigrimanum* | 0 | 0 | 0 | 1 | 3 | 1 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 |
| *S. chalcocoma* | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | 1 | 0 | 2 | 2 | 1 | 1 | 0 |
| *S. huairayacu* | 0 | 0 | 0 | 2 | 3 | 0 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 |
| *S. lahillei* | 0 | 0 | 0 | 2 | 2 | 0 | 2 | 1 | 0 | 2 | 1 | 1 | 0 | 2 | 2 | 1 | 1 | 0 |
| *S. scutistriatum* | 0 | 1 | 0 | 2 | 3 | 2 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 |
| *S. hirtipupa* | 0 | 1 | 0 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 |
| *S. orbitale* | 0 | 1 | 0 | 2 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 |
| *S. guianense* | 0 | 1 | 0 | 1 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 |
| *S. itaunense* | 0 | 1 | 0 | 2 | ? | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 1 |
| *S. perplexum* | ? | ? | ? | ? | ? | ? | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1+2 | 0 | 0 | 0 |

| | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *PARAAUSTROSIMULIUM* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *NEVERMANNIA* | 3 | 0+1 | 0 | 0 | 0 | 0+1 | 0+1 | 0 | 2 | 1 | 1+2 | 0 | 0 | 0+2 | 0+1 | 0 |
| *POMEROYELLUM* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0+1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 |
| *PTERNASPATHA* | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *S. oviedoi* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *HEMICNETHA* | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| *HEARLEA* | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| *ANASOLEN* | 0 | 0 | 0 | 0 | 0 | 0+1 | 1 | 0 | 0 | 0+1 | 1 | 0 | 0 | 0 | 0 | 0 |
| *XENOSIMULIUM* | 2 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0+1 |
| *FREEMANIELLUM* | 2 | 1 | 0 | 1 | 0 | 0 | ? | 0 | 1 | 1 | 2 | 1 | 0 | 1 | 0 | 1 |
| *S. muiscorum* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | – |
| *S. sumapazense* | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | – |
| *S. wygodzinskyorum* | ? | ? | 1 | 0 | 1 | 1 | ? | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | – |
| *S. nigrimanum* | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | – |
| *S. chalcocoma* | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | ? | ? | ? | ? | ? | ? | ? |
| *S. huairayacu* | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | – |
| *S. lahillei* | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | – |
| *S. scutistriatum* | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 1 | 0 | 0 | 1 | – |
| *S. hirtipupa* | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | – |
| *S. orbitale* | ? | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | – |
| *S. guianense* | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | – |
| *S. itaunense* | 2 | ? | 0 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | – |
| *S. perplexum* | 2 | 1 | 0 | 1 | 1 | ? | 1 | 1 | ? | 0 | 1 | 0 | 1 | 2 | 1 | – |

sidered noxious to humans; *lahillei* bites humans and cattle (Coscarón, 1991).

This research attempts to solve three questions. Is *Trichodagmia* (*sensu* Crosskey & Howard, 1997) monophyletic? Are *Trichodagmia* and *Thyrsopelma* (*sensu* Coscarón, 1987) monophyletic? What are the relationships between *Trichodagmia* and *Thyrsopelma* (*sensu* Coscarón, 1987)? These questions must be answered in order to address the correct nomenclatural position of these taxa.

## MATERIAL AND METHODS

In broad terms, we use the method of phylogenetic systematics as outlined in Kitching *et al.* (1998). Outgroup comparisons were performed following Nixon & Carpenter's (1993). The data matrix included 2 terminal taxa: 13 species of *Trichodagmia sensu* Crosskey & Howard (1997) and exemplars representing the subgenera *Anasolen, Freemaniellum, Xenosimulium, Hearlea, Hemicnetha* and the *oviedoi* species group as an ingroup. The latter were included to test the putative sister-group relationship between *Trichodagmia* and *Thyrsopelma*. Four outgroups were included: the genus *Paraustrosimulium* and the subgenera *Simulium* (*Pternaspatha*), *Simulium* (*Nevermannia*) and *Simulium* (*Pomeroyellum*).

Character codings for *Paraustrosimulium* were based on *Paraustrosimulium anthracinum*; for *S.* (*Pternaspatha*) on *S. nemorale, S. nigristrigatum* and *S. diamantinum*; for *S.* (*Anasolen*) on *S. masabae, S. nili* and *S. dentulosum*; for *S.* (*Freemaniellum*) on *S. berghei*; for *S.* (*Xenosimulium*) on *S. neireti*; for *S.* (*Hearlea*) on *S. larvispinosum, S. carolinae* and *S.*

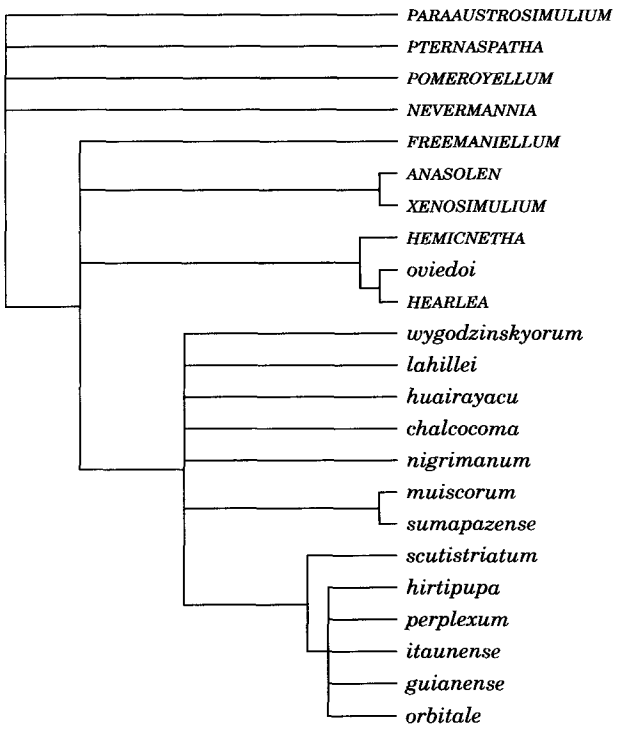


**Figure 1.** Consensus of nine trees found under equal weights (101 steps, CI 0.49, RI 0.73).

*capricornis*; for *S.* (*Hemicnetha*) on *S. mexicanum* and *S. paynei*; for *S.* (*Nevermannia*) on *S. loutetense*, *S. ruficorne* and *S. brachium*; for *S.* (*Pomeroyellum*) on *S. alcocki*, *S. shoutedeni* and *S. cervicornutum*; for *S. oviedoi* on *S. oviedoi* and *S. rivasi*. Terminals representing these genera, subgenera and groups were thus composite codings, based on 1–3 species.

Thirty-four morphological characters were used in the analysis. Six were based on larval morphology [0–5]; five on pupal morphology [6–10], 16 on adult female morphology [11–26]; and seven on adult male morphology [27–33]. Character codings were drawn from the original descriptions, redescriptions by Dalmat (1955), Crosskey (1960, 1969), Py-Daniel, Konrad & Gastal (1985), Coscarón (1991), Muñoz (1996) and Shelley *et al.* (1997) and original observations from additional specimens (Appendix). Table 1 gives descriptions of characters and states. The matrix itself appears in Table 2. All multistate characters were treated as unordered to minimize assumptions of character order.

We performed the analysis under equal weights and successive weighting with Paup* 4.0d64 (Swofford, 1998). Tree branches were collapsed if minimal branch length was equal to zero (rule 1, Swofford & Begle, 1993; Coddington & Scharff, 1994). We used the heuristic search option in PAUP*, randomizing the taxa addition order 100 times. Tree choice was also based on successive weighting using the maximal rescaled consistency index (Farris, 1989). We used implied weights as an alternative weighting approach (Goloboff, 1993). We used Peewee version 3.0 (Goloboff, 1998) with a similar search strategy: 100 random addition sequences using time as the random seed [amb-; rseed0; bound*100; max* commands], under all concavity values between three and six. Character distribution was examined with Clados version 1.6 (Nixon, 1996) and with Winclada version 0.9.99i (Nixon, 1999) under the unambiguous reconstruction option.

To calculate Bremer support values (Bremer, 1988) we used the relative Bremer support as calculated with Nona program (Goloboff, 1998). The characters were weighted according to the final cladogram using successive weighting. To obtain Bremer support values, we used the bsupport* option with a value of 400 steps.

To test the concordance of life stages as proposed by Judd (1998), we performed three tree searches with equal weights, each one based on data from a different life stage (larva, pupa or imago), and calculated the Incongruence Index (Mickevich & Farris, 1981) as proposed by Judd (1998). We also calculated the Incongruence Length Difference (Farris *et al.*, 1994) between pairs of matrices, as implemented in Winclada (Nixon, 1999), using 1000 permutations and mult*10; max* as the tree search strategy.

## RESULTS AND DISCUSSION

### EQUAL WEIGHTS VS. WEIGHTED DATA

PAUP* with equal weights found nine equally parsimonious trees (length 101 steps CI 0.49 RI 0.73), the strict consensus of which is shown in Figure 1. Successive weighting on this solution set chose one of the nine cladograms (Fig. 2: 31.37 steps CI 0.62 RI 0.87 total $fit_{con3} = 235.8$). Implicit weights with concavity values of 3–6 all gave the same two trees, one of which was identical to Figure 2. Figure 2 is thus the only topology favoured by equal, successive, and implied weights.

*Thyrsopelma sensu stricto* is monophyletic in the strict consensus (Fig. 1), but the monophyly of *Trichodagmia* is not supported unambiguously by this analysis. Both taxa were supported by successive weights and in both trees under implied weights.

The support for two groups in particular is suspect. The relationship between *Hemicnetha*, *Hearlea* and the *oviedoi* group (Fig. 1) is supported by a claw with a small denticule (character 13), which could be considered a convergence because *Nevermannia*, *Anasolen*, *Xenosimulium* and many species of *Trichodagmia* and *Thyrsopelma* have the same character. Likewise, *Hearlea* and the *oviedoi* group (Fig. 1) are united by the basimere length/width ratio (character 27); this possibly is also a convergence.

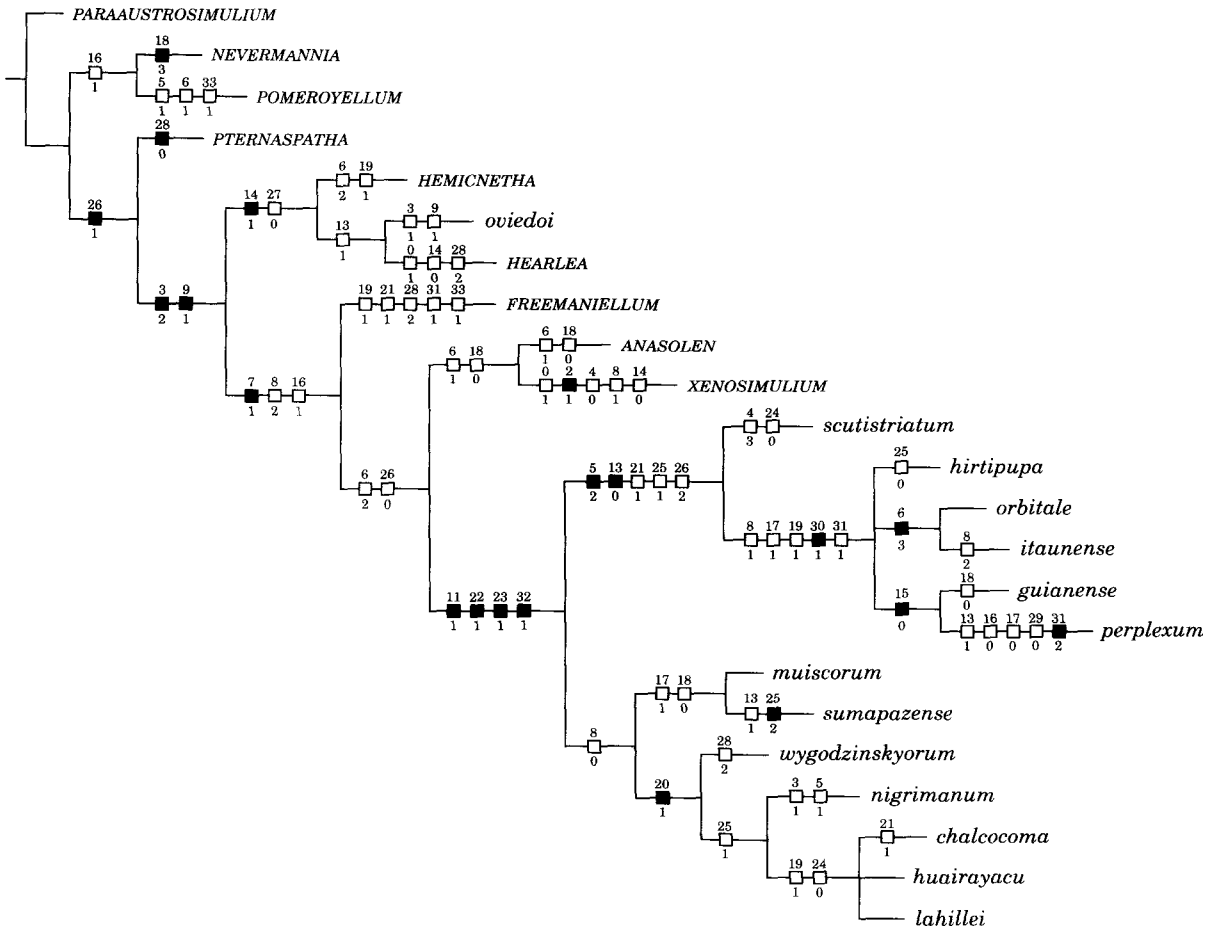


**Figure 2.** Cladogram preferred by successive weights and implicit weights under concavity values 3–6 (final length 31.37, steps CI 0.62, RI 0.87, total $fit_{con3} = 235.8$; with equal weights it has a length of 101 steps).

### BRANCH SUPPORT

Relative Bremer support values (fig. 3) are comparatively high for the ingroup. The highest Bremer support values is for *Thyrsopelma* + *Trichodagmia*, the subgenus *Thyrsopelma*, the '*nigrimanum* species group', and '*hirtipupa* + *orbitale* species groups'. The value for *Trichodagmia*, although low, does not necessarily indicate a non-natural group.

### COMBINED VS. PARTITIONED DATA

The life stage partitions of the data all gave more ambiguous results. The larval data set gave many most parsimonious trees (length 18) and a bush as the consensus. The pupa data set was similar (length 13) and a bush as the consensus. The adult data set under equal weights produced 225 trees (length 62), the consensus of which is shown in Figure 4. Larval and pupal stage results are not consistent with the combined cladogram whereas the consensus of the adult results is congruent with the cladogram (Fig. 2). These results are expected because the adult partition has more characters than larval or pupal stages alone or combined, and most of the synapomorphies in Figure 2 are adult characters. Judd (1998) also found that the partition with more characters (in her case, the larval dataset) gave the most resolution, and was most compatible with the combined analysis.

Combined analysis cannot give a result shorter than the sum of the partitioned lengths (93 steps = 18 + 13 + 62). In fact, the minimum length for the combined data set was 101, indicating 8 steps (7.9%) attributable to incongruence, but this value is not significant using ILD with any pair of matrices (Table 3). Our analyses show that a combined analysis gives a more resolved result than any of the partitions, which indicates, as advocated by Hennig (1968), that the holomorphology is highly recommended in cladistic analysis, because one does not know *a priori* in which stage the synapomorphies will occur.

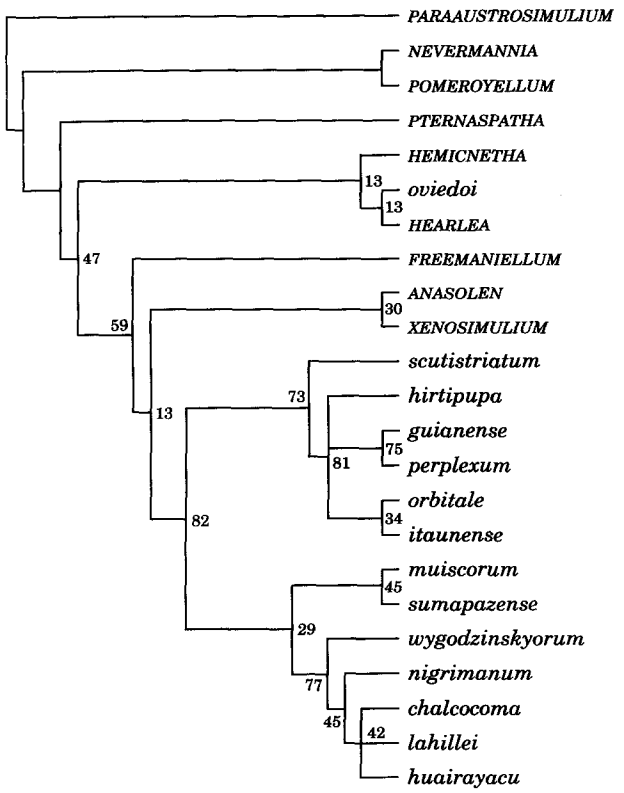


**Figure 3.** Cladogram showing relative Bremer support.

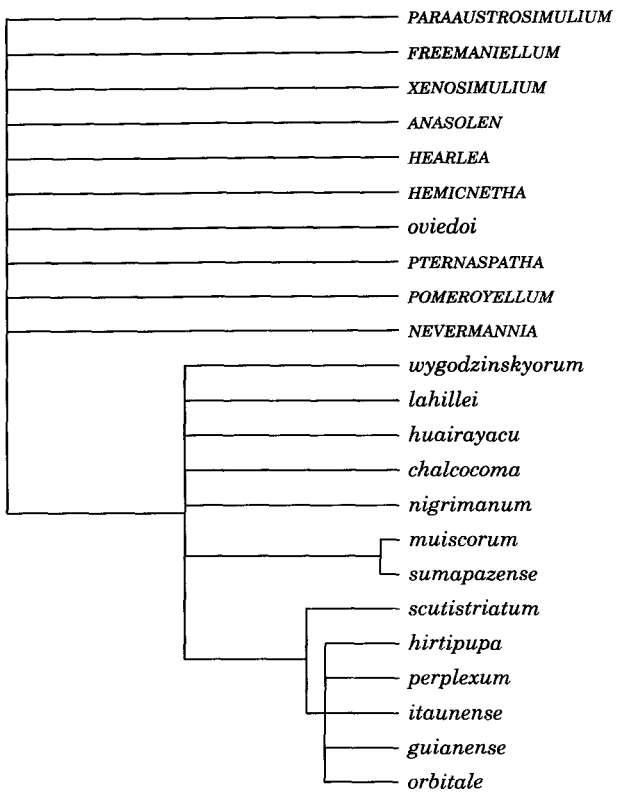


**Figure 4.** Consensus of 225 trees yielded for the adult partition analysis, equal weighted characters (initial trees of 62 steps CI 0.50, RI 0.78).

TOPOLOGY AND CHARACTER ANALYSIS

Cladistic analysis corroborates *Trichodagmia* monophyly (Crosskey & Howard, 1997), *Trichodagmia sensu stricto* and *Thyrsopelma* monophyly (Coscarón, 1987), and their sister relationship (Coscarón, 1987). *Trichodagmia* + *Thyrsopelma* is supported by the wide genital fork arms (character 22), lacking a prominent internal projection (character 23, Coscarón (1987: fig. 10A,C)), and endoparameres without or with reduced spines (character 32, Coscarón (1987: fig. 13 I)). Coscarón (1987) proposed that the distimere shape is also a synapomorphy of this taxon, but the feature is also present in *Freemaniellum* (character 29, Coscarón (1987: figs 19D, 20B, 22E,F,H,I, and J), see also fig. 91 in Crosskey (1969)). This character initially suggested that *Freemaniellum* was the sister group of *Trichodagmia* + *Thyrsopelma*, but the current analysis suggests *Anasolen* + *Xenosimulium* as the sister group, based on the number of branchial filaments (character 6) and the gonapophysis length/width ratio (character 26).

The monophyly of *Thyrsopelma* rests on hypostomial teeth shape (character 1, Coscarón (1987, fig. 29H)), larval body tegument covered with lanceolated hairs (character 5, Coscarón (1987: fig. 30O)), female with simple claw (character 13), and gonapophysis size (character 26). *S.* (*Thyrsopelma*) *perplexum* has a claw with a small denticule but we consider this a reversion from the subgenus groundplan.

**Table 3.** Incongruence values. Incongruence Index (D) and Incongruence Length Difference (ILD) tests for all pairs of matrices. A = imago. P = pupa. L = larva. No values are statistically significant

| MATRICES | D | ILD |
|---|---|---|
| A−(L+P) | 101−(62+32)=7 | 0.3337 |
| A−P | 80−(62+13)=5 | 0.4216 |
| A−L | 84−(62+18)=4 | 0.8901 |
| L−P | 32−(18+13)=1 | 0.9600 |

Although this analysis corroborates the species groups proposed by Coscarón (1987), we prefer not to maintain them nomenclaturally in order to promote homogeneity, and in light of new proposals concerning specific/supraspecific nomenclature (Pleijel, 1999; Cantino *et al.*, 1999). The relations between the species of '*orbitale* species group' require further work to solve the present soft polytomy, perhaps using chromosomal and/or molecular characters, or the discovery of the

larval stage of *perplexum* and the female of *itaunense*.

*Trichodagmia* is also monophyletic, based on the branchial tip sclerotization (character 8, Coscarón (1987: fig. 25E)). Coscarón (1987) used neither this character nor the branchial tip form. An additional synapomorphy is cibarial teeth in the female (character 11, Coscarón (1987: figs. 5N,O)). Shelley *et al.* (1997) reported that the cibarium of *S. guianense* and *S. perplexum* was unarmed, but in fact their cibaria bear small tubercules (character 12, Shelley *et al.* (1989: figs. 3, 4), Shelley *et al.* (1997: fig. 56)). Coscarón (1987) proposed that the gonapophysis length/width ratio (character 26) was also a synapomorphy of *Trichodagmia*, and, although a similar ratio in *Anasolen* and *Xenosimulium* does not preclude the character as an homology, we prefer not to use it.

We synonymize the '*lahillei*' and '*nigrimanum* species groups' proposed by Coscarón (1987) because *S. wygodzinskyorum*, although originally placed in the *lahillei* group (Coscarón and Py-Daniel, 1989), was basal to the clade.

*Trichodagmia* and *Thyrsopelma* species breed in fast-flowing creeks, also in rivers or in high-speed streams. The African taxa *Xenosimulium–Anasolen–Freemaniellum* live in similar places and one might consider the similarity ecologically convergent. However, there is extensive phylogenetic congruence between characters in the cladogram (see Fig. 2), and other Neotropical taxa (*Hemicnetha, Chirostilbia, Ectemnaspis*, or *Psaroniocompsa*) breed in the same places. Instead we regard these similarities as synapomorphies rather than convergences.

Crosskey (1969) proposed a possible relationship between *Trichodagmia* and *Xenosimulium/Anasolen/Freemaniellum*, but he considered *Xenosimulium* more likely to be related to *Freemaniellum–Anasolen* than to *Trichodagmia*. This analysis suggests that *Anasolen/Xenosimulium* is closer to *Thyrsopelma/Trichodagmia* than to *Freemaniellum*. *Anasolen/Xenosimulium* is the sister group of *Thyrsopelma* + *Trichodagmia*. Nevertheless, additional research using chromosomal and/or molecular data may support *Freemaniellum* as sister to *Trichodagmia* + *Thyrsopelma*. Coscarón (1987) proposed *Hemicnetha* as sister to *Thyrsopelma* + *Trichodagmia*, but that hypothesis fails when the Afrotropical subgenera *Xenosimulium*, *Anasolen* and *Freemaniellum* are included.

We found a possible sister group relationship between *Nevermannia* and *Pomeroyellum*, but character support for it is weak. Craig (1997) studied the *Inseliellum* subgenus and found good support for *Inseliellum* as sister to *Nevermannia*, although we did not include that subgenus in our research. *Nevermannia*'s cladistic definition and its sistergroup relationship await further research.

## CLASSIFICATION

Based on the relationships depicted in the cladogram we propose the following classification:

1. Subgenus *Trichodagmia*
   - 1.1. *S. muiscorum*
   - 1.1. *S. sumapazense*
   - 1.3. *S. wygodzinskyorum*
   - 1.4. *S. nigrimanum*
   - 1.5. *S. chalcocoma*
   - 1.6. *S. huairayacu*
   - 1.7. *S. lahillei*
2. Subgenus *Thyrsopelma*
   - 2.1. *S. scutistriatum*
   - 2.2. *S. hirtipupa*
   - 2.3. *S. orbitale*
   - 2.4. *S. guianense*
   - 2.5. *S. perplexum*
   - 2.6. *S. itaunense*

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## APPENDIX: SPECIMENS STUDIED

BMNH: The Natural History Museum, London. UK.
ICN: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia.
MLP: Museo de la Plata, Universidad Nacional de La Plata, La Plata, Argentina.

*S. chalcocoma*

PERU: Sariepanga, Depto Huanuco 46.360 m.a.s.l. (sic). female genitalia, specimen pinned coll. Feliz Woytkowski [MLP]. E. Central, Pichita Caluga. 2200 m. Female slide 17.viii.1959 coll. P. Wygodzinsky [MLP]. Machupichu. Female over man. 18.iv.1971. Col. Halfter [MLP]. Cuzco, Machupichu 2300 m. Female slide. 21–24.x.1972. Coll. P. Wygodzinsky [MLP].

*S. guianense* (as *S. pintoi)*

BRAZIL: Roraima, 28.x.1987, female in slide, Coll. No data [MLP]. Goias, Caldas Novas, viii.94 over a cow, female in slide, coll. Júlio [MLP]. Para, Río Curuá-Una, Cachoeira do Palhao. 16.ii.1968, female in slide, coll. No data [MLP]. Roraima. Mujacai mission, 28.x.1977, male in slide, coll. A.J. Shelley det. Shelley [MLP]. Roraima, Río Uraricoera, 23.x.1987, male in slide Coll. S. Coscarón [MLP]. Nova Teutonia, 27°11′B 52°23′L 300–500 m, vii.1970, male in slide Coll. Fritz Plauman [MLP]. Sao Pablo, Ibiti, 23.iv.1946, pupa exhuviae in slide, Coll. J.L. Lima [MLP]. Sao Pablo, Piracicaba, pupa exhuviae, coll. no data det. Andretta [MLP]. Roraima Cach. Morurí river, 23.x.1987, larva, coll. No data [MLP]. Roraima, Río Uraricoera, 23.x.1987, larva, coll. S. Coscarón [MLP]. Sao Pablo, Piracicaba, 1945, larva, coll. no data det. Andretta [MLP].

*S. hirtipupa*

BRAZIL: Bahia, near to Itabuna, Oricó river, female + pupa (two slides). 31.vii.1986 coll. no data [MLP]. Sao Pablo. Faz, Barra do Turba. Male in slide. 30.viii.1979, coll. S. Coscarón [MLP]. Sao Pablo. Faz, Barra do Turba, exhuvia, 30.viii.1979, coll. S. Coscarón [MLP]. Bahia, near to Itabuna, Río Oricó, larva, 31.vii.1986, coll. no data [MLP].

*S. huairayacu*

ARGENTINA: Tucumán, Hulinchay ruta 311. 17.x.73. Female slide. Coll. S. Coscarón [MLP]. Tucumán, Hulinchay ruta 311. 17.x.1973. Male slide. Coll. S. Coscarón [MLP] Jujuy, Tilia, Garganta del Diablo. ix.1962. Pupa pharate. coll. P. Wygodzinsky [MLP] Salta, Río Lorenzo. 11.vi.73. Two larvae. Coll. S. Coscarón [MLP]. Bolivia: Moraya, 11.xii.65. Female. Coll. S. Coscarón [MLP].

*S. lahillei*

ARGENTINA: Tucumán, Quebrada de Lules, 25.viii.1948, female in slide, coll. P. Wygodzinsky [MLP]. Tucumán, Siambón, 20.x.1973, female in slide, coll. S. Coscarón [MLP]. San Juan, San Juan, Valle Fertil, female in slide, 10.xi.1967, coll. S. Coscarón [MLP]. Tucumán, Quebrada de Lules, 15.viii.1948, male in slide, coll. P. Wygodzinsky [MLP]. Tucumán, Siambón, 20.x.1973, male in slide, coll. S. Coscarón [MLP]. La Rioja, Chilecito, Rio Sañogasta, 2.xi.1967, male in slide coll. no data [MLP] Salta, Cuesta del Obispo, Arroyo Maray, 13.iii.1992, male in slide, coll. S. Coscarón [MLP]. Jujuy, Garganta del diablo, Tilcara, ix.1962, male in slide, coll. S. Coscarón [MLP]. Jujuy, Garganta del diablo, Tilcara, ix.1962, exhuvia in slide, coll. S. Coscarón [MLP]. Tucumán, Siambon, larva in slide, x.73, coll. S. Coscarón [MLP]. Cordoba, Ceballos river, larva in slide [MLP]. PERU: Miraflores, Rio Chirines 1200 m, female in slide, 3.viii.48, leq W. Weyrauch [MLP].

*S. muiscorum*

COLOMBIA: Cundinamarca, La Calera, Río Teusaca. 7.v.78. Male + Pupa. coll M. Bueno. cat. num. 1135 [ICN]. Cundinamarca, La Calera, Río Teusaca. 7.v.78. Male, Paratipo coll M. Bueno & L.I. Moncada. cat. num. 244 [ICN]. Cundinamarca, Usme, Chisacá, Las Ruinas. 18.viii.90. coll X. Martínez & A. Mejía. female + pupa. cat. num. 268 [ICN]. Cundinamarca, Usme, Chisacá, Las Ruinas. 18.viii.90. coll X. Martínez & A. Mejía. female + pupa. cat. num. 269 [ICN]. Cundinamarca, La Calera, Río Teusaca. 27.xi.77. coll. P. Muñoz. Female. cat. num. 1131 [ICN]. Cundinamarca, Usme, Chisacá, Río Chisacá. 9.v.87. coll J. Campos. Female. cat. num. 267 [ICN]. Cundinamarca, Aguadita, Rio Blanco. 20.ii.95. Female. cat. num. 2247 [ICN]. Cundinamarca. La Calera, Río Teusaca, El Hato. 2.iv.1977. Coll. M. Bueno Larva. Cat # 1177 [ICN]. Cundinamarca. La Calera, Río Teusaca, El Hato. 28.ix.1976 Coll. M. Bueno. Larva. Cat # 1126 [ICN]. Cundinamarca. La Calera, Río Teusaca. 27.iv.1976. Coll. M. Bueno. Larva. Cat # 1125 [ICN].

*S. nigrimanum*

BRAZIL: Sao Pablo, Sto Amaro, Clube Indiano, 24.v.68, female + pupa, coll. Vulcano. [MLP]. Goyas S.F. Chagas, female [MLP]. Campinas, female in slide [MLP]. Minas Gerais, Ribeirado Castelimbo, 4.x.1986, male in slide coll. S. Coscarón [MLP]. D.F. Rio Descoberto, 8.vi.76, male in slide, coll. A.J. Shelley [MLP]. Sao Pablo, Sto Amaro, Clube Indiano, 9.vi.68, male and pupa in slide, coll. Vulcano [MLP]. Sao Pablo, Chavantes, Corrego Monjolimho, 18.x.1986, larva in slide, coll. S. Coscarón [MLP]. C. de Jordao, La Amalia, 12.ix.1985, larva in slide, coll. S. Coscarón [MLP]. Sao Paulo, Sta. Rosa de Viterbo, Rio Pardo, ix.1985, larva in slide, coll. S. Coscarón [MLP].

*S. orbitale*

ARGENTINA: Entre Ríos, El Palmar, 11.vii.1978, female in slide, coll. J. Williner [MLP]. Entre Ríos, Salto grande, 16.i.1974, female in slide, coll. S. Coscarón [MLP]. Misiones Iguazu river, Cataratas, 10.xi.1980 two males in slide, coll. S. Coscarón [MLP]. Misiones, Río Iguazu, Cataratas, 17.x.74, male, coll. S. Coscarón [MLP]. Misiones, Magdalena stream, road to Oberá, 30.x.81, male in slide, coll. S. Coscarón [MLP]. Corrientes, Paraná river, 24.ix.1992, exhuvia, coll. S. Coscarón [MLP]. Buenos Aires, Quequen Salado, 3.xii.1993, exhuvia, coll. S. Coscarón [MLP]. Misiones Rio Iguazu, Iguazu falls area, 17.x.1979, larva, coll. S. Coscarón [MLP]. Misiones, Magdalena stream, road to Oberá, 30.x.81, larva, coll. S. Coscarón [MLP]. PARAGUAY: Caaguazú, Río Acaray, 12.vii.1971, male, coll. S. Coscarón [MLP]. Caaguazú, Río Acaray, 12.vii.1971, larva, coll. S. Coscarón [MLP]. BRAZIL: Roraima. Mujacai mission, 5.i.1977, female in slide, coll. A.J. Shelley det. Shelley [MLP]. Sao Pablo, Vale de Orixas, Usina, 1.v.1986, exhuvia, coll. S. Coscarón [MLP].

*S. perplexum*

BRITISH GUINEA: Kaieteur. Male in slide. Pupae on podostomataceae at lip of fall (paratype). 9.ix.1937, coll. Richards & Smart [BMNH]. Kaieteur falls, R. Potaro male (paratype). 9.ix.1937. coll. O.W. Richards & J. Smart [BMNH].

*S. scutistriatum*

BRAZIL: Minas Gerais, Serra Caraca, 1380 m, xi.1961, female in slide, coll. Martins & Silva [MLP]. Minas Gerais, Jaboticatuba, Río Capivara, Serra do Cipo, 4–9.vii.1979. males in slide, coll. I. Sazima [MLP]. Minas Gerais, Jaboticatuba, Río Capivara, Serra do Cipo, 4–9.vii.1979, pupa, coll. I. Sazima [MLP]. Minas Gerais, Jaboticatuba, Río Capivara, Serra do Cipo, 4–9.viii.1974, larva, coll. I. Sazima [MLP]. Sao Pablo, Valle do Coixas, 3.v.1986, larva, Coll. no data [MLP].

*S. sumapazense*

COLOMBIA: Cundinamarca, Páramo de Guasca, 3300 m, 20.vi.1967, coll. P Wygodzinsky, Paratype [MLP]. Cundinamarca, vía Bogotá-Choachí, Río Teusaca. 23.x.1993, female. coll P. Muñoz. cat # 1050 [ICN]. Cundinamarca, vía Bogotá-Choachí, Río Teusaca. 23.x.1993. Larva. coll P. Muñoz. cat # 1252a [ICN]. Cundinamarca, vía Bogotá-Choachí, Río Teusaca 3270 m. 23.x.1993. Larva. coll P. Muñoz. cat # 1035 [ICN]. Cundinamarca, Choachí. 14.xii.1993. Larva. coll P. Muñoz. cat # 1837 [ICN].

*S. wygodzinskyorum*

PERU: Junín, Estancia el Naranjal, San Ramón 1000 m. Male. 20.vii.1965 col. P. Wygodzinsky Paratype [MLP].

*Paraustrosimulium anthracinum*

CHILE: Chiloe, Rio Melilebu, entre Huillineo y Chonchi, 30.xi.1992, female in slide, coll. S. Coscarón [MLP]. Freire, Puente Mafil sobre panamericana, 23.xi.1992, female + pupa in slide, coll. S. Coscarón [MLP]. Chiloe, Rio Melilebu, entre Huillineo y Chonchi. 30.xi.1992, male + pupa in slide, coll. S. Coscarón [MLP]. Freire, Puente Mafil sobre panamericana, 23.xi.1992, larva in slide, coll. S. Coscarón [MLP]. ARGENTINA: Bariloche,

Playa Serena, 18.x.1984, female + pupa in slide, coll. S. Coscarón [MLP]. Tierra del Fuego, Isla de los Estados, xi.1965, female + pupa in slide, coll. A. Bachmann [MLP]. Bariloche, Playa Serena, 18.x.1984, male in slide, coll. S. Coscarón [MLP]. Tierra del Fuego, Isla de los Estados, xi.1965, male in slide, coll. A. Bachmann [MLP]. Chubut, El Triana, male in slide [MLP]. Tierra del Fuego, Ushuaia, Rio Oliva, 22.i. 1960, exhuvia, coll. S. Coscarón [MLP]. Bariloche, Playa Serena, 18.x.1984, larva in slide, coll. S. Coscarón [MLP].

*S.* (*Pternaspatha*) subgenus

*Simulium nemorale*

ARGENTINA: Rio Negro, Ruca Malén, 30.xi.1950 2 females + 1 exhuvia, coll. P. Wygodzinsky [MLP]. Rio Negro, Gutierrez lake, 30.xii.1992, pupa pharate + larva, coll. S. Coscarón [MLP]. Chubut, Futalufquen, near YPF, 24.i.1993, larva, coll. S. Coscarón [MLP]. Río Negro, El Bolsón, Quequen Treu river, 24.i.1993, larva, coll. S. Coscarón [MLP].

*S. nigristrigratum* (as *S. bachmanni*)

ARGENTINA: Neuquen, Limay river, 23-Y-1968, female + pupa in slide, coll. S. Coscarón [MLP]. Río Negro, Chimpay – Art, 30.xi.1993, female + pupa in slide, coll. S. Coscarón [MLP]. La Pampa, 25 de Mayo, Canal entrada Centelle, 18.xii.90, female in slide, coll. H. Marino [MLP]. Chubut, 28 de Julio, Canal Sur, 15.i.1993, male + pupa in slide, coll. S. Coscarón [MLP]. Río Negro, Col. M. Elvera, 6.i.1994, male in slide, coll. S. Coscarón [MLP]. Neuquen, chas Malal, río Currileufú, 21.i.1968, exhuvia in slide, coll. S. Coscarón [MLP]. Neuquen, Limay river, 23.i.1968, larva in slide, coll. S. Coscarón [MLP].

*S. diamantinum*

ARGENTINA: Mendoza, Diamante river, 3300 m, 28.i.1995, female in slide, coll. S. Coscarón [MLP]. Neuquén, Buta Ranquil, 22.ix.1975, female in slide, coll. S. Coscarón [MLP]. Neuquén, Buta Ranquil, 22.ix.1975, male in slide, coll. S. Coscarón [MLP]. Neuquén, Buta Ranquil, 3 Km al Sur, 22.ix.1975, exhuvia in slide, coll. S. Coscarón [MLP]. Mendoza, Diamante river, 3300 m, 28.i.1995, larva in slide, coll. S. Coscarón [MLP].

*S.* (*Anasolen*) subgenus

*Simulium masabae*

UGANDA: Sifri, 3.v.1932, female in slide, paratype, coll. E.G. Gibbins [BMNH] cat # 1943-20. Sifri, 3.v.1932, female in pin, paratype, coll. E.G. Gibbins [BMNH] cat # 1943-20. Lule, Buhishu, 1.iv.1932, female in pin, paratype, coll. E.G. Gibbins [BMNH] cat # 1943-20. Sifri, 3.v.1932, male in slide, paratype, coll. E.G. Gibbins [BMNH] cat # 1943-20. Sifri, 3.v.1932, male in pin, paratype, coll. E.G. Gibbins [BMNH] cat # 1943-20. Pupal pelt, coll. E.G. Gibbins [BMNH]. Kapehorisa, Mt Elgon, Tabok river, 6600 ft. 18.x.1964, larva in alcohol, coll. R. Crosskey [BMNH].

*S. nili*

UGANDA: Juinja (R. Nile), 4.iii.1932, female in slide, paratype, coll. E.G. Gibbins [BMNH] Brit. Mus. cat # 1943.20. Juinja (R. Nile), 4.iii.1932, female in pin, paratype, coll. E.G. Gibbins [BMNH] Brit. Mus. cat # 1943.20. Juinja (R. Nile), 4.iii.1932, male in slide, paratype, coll. E.G. Gibbins [BMNH] Brit. Mus. cat # 1943.20. Juinja (R. Nile), 4.iii.1932, female in pin, paratype, coll. E.G. Gibbins [BMNH] Brit. Mus. cat # 1943.20. SAUDI ARABIA: Asir prov. J Suda 2550 m, 5.x.1980, 2 pupae in alcohol, coll W. Bütti Ker [BMNH]. Asir prov. J Suda 2550 m, 5.x.1980, 2 larvae in alcohol, coll W. Bütti Ker [BMNH].

*S. dentulosum*

UGANDA: Lule Bugishu, 1.iv.1932, female in slide, coll. E.G. Gibbins [BMHN]. Bevamba pass, 17.xi.1931, female in pin, coll. E.G. Gibbins [BMHN]. R. Sifi, 7000 ft, 3.v.1932, male in slide, coll. E.G. Gibbins [BMHN] Lule Bugishu, 1.iv.1932, male in pin, coll. E.G. Gibbins [BMHN]. 25.xii.1934, pupa in slide [BMNH]. Ruwenzori, Trib of Mahoma river, 2200 m. larva in slide. [BMNH].

*S.* (*Freemanellum*) subgenus

*Simulium berghei*

NIGERIA: Kamartan, Mambilla Plateau, Forest Reserve, 10.xii.1968, female in slide, coll. H. Roberts [BMNH]. Kamartan, Mambilla Plateau, Forest Reserve, 10.xii.1968, female in pin, coll. H. Roberts [BMNH]. Kamartan, Mambilla Plateau, Ngel Nyaki, Montane forest c. 5500 ft. uv. Light. 28.xi.–3. xii.1968, female in pin, coll. J.C. Deeming [BMNH]. Kigrzi, larva in slide, [BMNH]. BELGIAN CONGO: Lturi, pupa + male genitalia in slide, coll. A. Fain [BMNH].

*S.* (*Xenosimulium*) subgenus

*Simulium neireti*

MADAGASCAR: Tsaratanana, 1200–1400 ft, 28.xi.1907, female in slide, coll. W.C. Holden [BMNH]. Andranolaya, x.1907, female in pin, coll. Lloyd [BMNH].

*S.* (*Hearlea*) subgenus

*Simulium larvispinosum*

GUATEMALA: XXII, female in slide [MLP]. XXII, male in slide [MLP]. XXII, 2 larvae in slide [MLP].

*S. carolinae*

GUATEMALA: Río Santa Anita, Finca Monte de Oro, 900 m, female in slide [MLP]. Río Santa Anita, Finca Monte de Oro, 900 m, male in slide [MLP].

*S. capricornis*

GUATEMALA: Acatenango, Chimalt'go Guate. 3.iv.1949, female in slide, coll. H.T. Dalmat [MLP]. Acatenango, Chimalt'go Guate, 26.xi.1949, female in slide, coll. H.T. Dalmat [MLP].

*S.* (*Hearlea*) spp.

Two exhuvias without data [MLP].

*S.* (*Hemicnetha*) subgenus

*Simulium mexicanum*

COLOMBIA: Cauca, Lopez de Micay, Qda. Angostura, 16.v.1977, female in slide, cat # 289, coll. P. Muñoz [ICN]. Valle, Cartago, Qda. La Colorada, 27.ii.1996, female + pupa in slide, cat # 2273, coll. C. Moreno [ICN]. Quidio, Quimbaya, Qda. Buenavista, 1100 m, 27.ii.1996, male in slide, cat # 2436, coll. C. Moreno [ICN]. Nariño, Mataje river, El Salto, 16.viii.1995, male in slide, cat #

1884b, coll. P. Muñoz [ICN]. Cauca, Lopez de Micay, Qda Angostura, 16.v.1977, exhuvia in slide, cat # 286, coll. P. Muñoz [ICN]. Cauca, Lopez de Micay, Quebrada Salto Nuevo, 21.viii.1977, larva in slide, cat # 1594d, coll. V. Ochoa [ICN]. Nariño, Tumaco, Balleneto Aduana, 25.vii.1995, larva in slide, cat # 1876b, coll. B. Sinisterra [ICN].

*S. paynei*

COLOMBIA: Valle, Norte de Dagua, 1200 m, 26.viii.1967, female in slide, coll. P. Wygodzinsky [MLP]. Cundinamarca, Río Dulce, 3 Km Norte de Alban, 8.viii.1967, female in slide, coll. P. Wygodzinsky [MLP]. Valle, Delfina, 400–500 m, 26.viii.1967, male in slide, coll. P. Wygodzinsky [MLP]. Cundinamarca, Río Dulce, 3 Km Norte de Alban, 8.viii.1967, larva in slide, coll. P. Wygodzinsky [MLP]. Venezuela: Merida, 2200 m, 6.x.1980, female in slide, coll. S. Coscarón [MLP]. Merida, 2200 m, 6.x.1980, larva in slide, coll. S. Coscarón [MLP]. GUATEMALA: Acatenango, Chimaltenango Guate, male in slide, coll. HT Dalmat [MLP]. XXXII. exhuvia [MLP].

*S. (Nevermannia)* subgenus

*Simulium loutetense*

EQUATORIAL GUINEA: Bioko. R. Musola at Musola Village, 30.iv.1996, exhuvia in slide, coll. P.J. McCall [BMNH]. R. Musola at Musola Village, 30.iv.1996, pupa in alcohol, coll. P.J. McCall [BMNH]. R. Musola at Musola Village, 30.iv.1996, larva in slide, coll. P.J. McCall [BMNH]. R. Musola at Musola Village, 30.iv.1996, larva in alcohol, coll. P.J. McCall [BMNH]. W. CAMEROON: Kumba, viiii. ix.1968, female in slide, coll. R.H. Disney, [BMNH]. Kumba, viii.ix.1968, male in slide, coll. R.H. Disney, [BMNH].

*S. ruficorne*

Niger: S. of Simia Air mountains Timia Stream, 13.i. 1983, exhuvia in slide, coll. J. Grunshaw [BMNH]. of Simia Air mountains Timia Stream, 13.i.1983, pupa in alcohol, coll. J. Grunshaw [BMNH]. S. of Simia Air mountains Timia Stream, 13.i.1983, larva in slide, coll. J. Grunshaw [BMNH]. S. of Simia Air mountains Timia Stream, 13.i.1983, larva in alcohol, coll. J. Grunshaw [BMNH]. MALI: Sikasso, 1–23.ix.1977, female in pin, WHO/OCP [BMNH]. N. NIGERIA: Zaria, Samaru, mv trap, male in pin, 25.ii.1966, coll. Deaming [BMNH].

*S. brachium*

KENYA: iv.–v.1960, female pharate + pupa in slide, coll. J.P. McMahon [BMNH]. iv.–v.1960, pupa in alcohol, coll. J.P. McMahon [BMNH]. iv.–v.1960, larva in slide, coll. J.P. McMahon [BMNH]. iv.–v.1960, larva in alcohol, coll J.P. McMahon [BMNH]. UGANDA: Bumboi Bugishu, 28.iii.1932, male in pin, coll. EG Gibbins [BMNH].

*S. (Pomeroyellum)* subgenus

*Simulium alcocki*

CAMEROON: R. Mungo Area. Vvi.1963. Female slide + female in alcohol. Coll. R.H. Disney [BMNH]. R. Mungo Area. vi.1963. Male slide + male in alcohol. Coll. R.H. Disney [BMNH]. Bioko: R. Sampara. 8.iv.1996. Pupa slide + pupa in alcohol. Coll. P.J. McCalb. [BMNH]. R. Sampara. 8.iv.1996. larva slide + larva in alcohol. Coll. P.J. McCalb [BMNH].

*S. shoutedeni*

N. NIGERIA: Abuja, male pharate and pupa in slide, coll. R.W. Crosskey [BMNH]. Abuja, pupa in alcohol, coll. R.W. Crosskey [BMNH]. GUINEA: Gebéssékéré. 3.iii.1963. Two larvae in alcohol, coll. R. Garms. [BMNH]. CONGO: Barringville, three males in pin, coll. A. Fain [BMNH]. GOLD COAST: female in pin, coll. MH Hughes, [BMNH].

*S. cervicornutum*

NIGERIA: Togo: Benin. 13–18.ix.1984. female in alcohol, coll. R.A. Cheke [BMNH]. Benin. 13–18.ix.1984. male in alcohol, coll. R.A. Cheke [BMNH]. KENYA: Nyanza, iv.–v.1960, Pupa + pharate male in slide, col. J.P. MacMahon [BMNH]. Nyanza, i.v–v.1960, Pupa in alcohol, coll. J.P. MacMahon [BMNH]. Nyanza, iv.–v.1960, larva in slide, coll: J.P. MacMahon [BMNH]. Nyanza, iv.–v.1960, larva in alcohol, col. J.P. MacMahon [BMNH]. SIERRA LEONE: Tonkolili District, Subonti State of Mabonto, 1.xii.1980, male in pin, coll. No data [BMNH]. Western Area, water course on Freetown, 23.xi.1980, male in pin, coll. No data [BMNH].

*Oviedoi group*

*S. rivasi*

VENEZUELA: Mérida, Páramo, 4100 m. 6.x.68. Female in slide, coll. Ramírez-Pérez [MLP]. Mérida. N. de apartaderos, 3850 m, male and pupa in slide: 13.ii.68, coll. J. Ramírez-Pérez [MLP]. Mérida. N. de Apartaderos. 3850 m, 13.ii.68, larva, coll. J. Ramírez-Pérez [MLP].

*S. oviedoi*

VENEZUELA: Mérida. N. de Apartaderos. 3850 m. 13.ii.68, female, coll. No data [MLP]. Mérida. Apartaderos-Sto. Domingo road, 3500 m, female in slide, 16/26.ii.68, coll. P. Wygodzinsky [MLP]. Mérida. Apartaderos-Sto. Domingo road, 3500 m. 16/26.ii.68, male, coll. P. Wygodzinsky [MLP]. Mérida. Apartaderos-Sto. Domingo road, 3500 m. 16/26.ii.68, larva, coll. P. Wygodzinsky [MLP].